The Role of Quaternary Spatiotemporal Gradients and Dynamic Disequilibrium in Shaping Present Neotropical biotic patterns

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1. Introduction

The longstanding myth of tropical climatic stability and its influence in the shaping of low-latitude biogeographical and ecological patterns was definitively dismantled in the mid-late 20th century, when the first evidence of Quaternary glacial-interglacial climate shifts were documented, and the corresponding biogeographical responses were reconstructed. Damuth & Fairbridge (1970) demonstrated the occurrence of severe arid conditions in Amazonia during the Last Glacial Maximum (LGM; ~21,000 years before present or ~21 ka BP). Working in the Amazon avifauna, Haffer (1969) proposed that LGM lowland forests would have been fragmented into isolated patches, or refugia, in a sea of savannas, thus favoring speciation and vicariance. From these refugia, the forests and the associated avifauna could have expanded during wetter interglacials, which would have promoted coalescence, thus favoring gene flow, competence, sympathric speciation and hybridization by secondary contact. Similar results were obtained by Vanzolini & Williams (1970) for lizards. Later, Prance (1982), Whitmore & Prance (1987) and Haffer & Prance (2001) summarized the occurrence of similar situations in other organisms and identified the purported lowland refugia based on present rainfall patterns and current species distribution.

However, further palynological work failed to find evidence for LGM aridity (Colinvaux, 1987; Colinvaux et al., 1996) and supported the continuity of lowland rainforests, although with different taxonomic composition due to the downward migration of montane species caused by cooling, moderate precipitation reduction and atmospheric CO_2 depletion. This was called the disturbance-vicariance hypothesis or DVH (Bush, 1994). Therefore, the refuge hypothesis (RH) was not needed to explain the biogeographical patterns observed in the Neotropical lowlands (Colinvaux et al., 2000). Following Gentry (1982), the proponents of the DVH emphasized the importance of the Andean uplift and the stability of the Amazon forests during the Neogene in the shaping of current Neotropical biogeography (Colinvaux & De Oliveira, 2001). In this framework, the Neotropical biotic patterns would have emerged during the Neogene and the Quaternary would have been a time of range reorganization and possibly of extinction (see also Wesselingh et al., 2010). This view was not shared by other paleoecologists working in the Neotropics (van der Hammen & Hooghiemstra, 2000), who maintained the initial Haffer's (1969) idea of wet refugia. The debate still persists and is centered on hydroclimatic patterns.

The advent of molecular DNA phylogenies revolutionized knowledge on Neotropical diversification and the number of studies supporting Neogene or Quaternary

Neotropical diversification flourished. A first metaanalysis including a wide range of organisms showed that extant Neotropical species originated in a continual fashion since at least the Miocene (>20 Ma) until the Pleistocene with no diversification bursts at any time period (Rull, 2008). Nearly the half of the analyzed species were Neogene in origin and the other half emerged during the Pleistocene. Similar results were obtained by Turchetto-Zolet et a., 2013) for a wide range of South American species. Therefore, it was proposed that the dual Neogene-Quaternary controversy did not make sense and current Neotropical biotic patterns resulted from a complex interplay of ecological and evolutionary processes across spatial and temporal scales, initiated by Neogene tectonics and continued under the action of Pleistocene climatic changes (Rull, 2011a, b). Examples of the spatiotemporal complexity of the origin and evolution of Neotropical biodiversity can be found in Hoorn & Wesselingh (2010), Hoorn et al. (2010), Antonelli et al. (2015, 2018) and Rull & Carnaval (2020), among others.

This paper is focused on the Quaternary, especially the last glacial cycle, from the LGM onward. This cycle is taken as a general model for the ~40 Pleistocene cycles of glacial-interglacial magnitude, which follow similar trends although with variations in intensity and duration (Raymo, 1994). The target areas are tropical South America, especially the Amazon/Orinoco lowlands, the Caribbean coasts and the Guiana Highlands (Fig. 1). Long paleoclimatic and paleoecological records from both terrestrial (Bogotá basin) and marine (Cariaco basin) (Fig. 1) settings demonstrate that Neotropical biomes and ecosystems were also affected by the glacial-interglacial cyclicity during the entire Pleistocene (e.g., Hooghiemstra, 1984; Haug et al, 1998; Yarincik & Murray, 2000; Torres et al. 2013). Unfortunately, similar records are unavailable for most Neotropical areas, including those studied here, where the last glacial cycle is widely represented and has been studied in more detail.

The main aim is to analyze some key spatiotemporal biotic gradients driven by Quaternary environmental shifts. In this context, the primary objective is to show how environmental forcing, mainly climatic changes and sea-level shifts, created different conditions for evolutionary, biogeographical and ecological interplay, in the shaping of current biomes and ecosystems. These observations are also discussed under the perspective of equilibrium dynamics of biotas and ecosystems, under the action of environmental forcing. The target areas and taxa (mostly vascular plants) to be studied have been chosen to gather a representative range of settings (coastal, lowland, montane), biomes (mangroves, rainforests, savannas, high-mountains) and ecological requirements (climate, topography, flooding, salinity tolerance), to assess the different biotic responses to environmental drivers. Another selection criterion has been the author's own experience in the study subjects, making extensive self-citation inevitable, although it has been substantially reduced.

2. An Iconic Neotropical Palm

Mauritia flexuosa is one of the most abundant and widely distributed palms across the Neotropics, with an estimated 1.5 billion individuals (ter Steege et al., 2013). It is able to develop in a diversity of vegetation types, such as rainforests, gallery forests, savannas, forest-savanna mosaics, and coastal forests, either as a forest component or in monospecific stands (Fig. 2). This lowland palm requires warm and wet climates and grows from nearly the sea level to ~1000 m elevation, usually in soils flooded by freshwater (riverbanks, lake shores, valley bottoms, coastal marshes), as it is salinity-intolerant (Vegas-Vilarrúbia et al. 2007). *M. flexuosa* has multiple uses for humans and has been part of indigenous cultures for long time. Some of these cultures refer to *M.*

flexuosa as the "tree of life". Fruits are the most valued resource, but almost every part of the palm has some utility for food, housing, ornamentation, fiber extraction, medicine or rituals, among many others. More details on *M. flexuosa* and its human uses in Rull & Montoya (2014) and Virapongse et al. (2017).

According to Bogotá-Ángel et al. (2021), the *Mauritia* ancestors originated in Africa during the Cretaceous and expanded to South America and India in the Paleocene. The global cooling of the Eocene-Oligocene transition (EOT) led to the extinction from India and a significant diversity reduction in Africa, from where it became extinct in the Oligocene. Therefore, *Mauritia* has been restricted to the Neotropics since the Miocene onward. Presently, *M. flexuosa* grows in the northern South American lowlands of the Orinoco, Amazon and adjacent basins, between approximately 12°N and 24°S (Fig. 3).

Over 40 sites within the current *M. flexuosa* distribution range, situated between near the sea level and 1040 m elevation, have been cored to reconstruct the Late Pleistocene-Holocene vegetation trends from pollen records (Fig. 4). The oldest record shortly antecedes the LGM and shows a few localities with *Mauritia* pollen, with two sites near 20°S with significant abundances. During the LGM, this pollen remained at the same sites but the percentages dropped to less than 1% in all of them. During the Lateglacial, the distribution expanded longitudinally and the percentages exhibit a slight recovery in some localities. The expansion and the percentage recovery accelerated during the rapid Early Holocene global warming (EHW) and a regional precipitation increase (Haug et al., 2001). The expansion reached its maximum in the Middle Holocene, during the Holocene thermal maximum (HTM), coeval with a precipitation maximum. In the Late Holocene, the abundance of *Mauritia* increased in the NW sector under stable temperatures, despite a significant regional drying shift (Haug et al., 2001). The role of humans as dispersal agents, especially during the last 2 ka, should not be disregarded. Human influence could have been manifested in active or passive fruit transport and also in selective burning of forests and savannas thus favoring *Mauritia* expansion (Rull & Montoya, 2014).

The whole picture would be consistent with postglacial expansion from scattered lowland LGM refugia, or microrefugia (Rull, 2009), where *Mauritia* could have survived during the last glaciation. While the biogeographical pattern seems to support the refuge hypothesis, the environmental drivers for glacial retraction and further postglacial expansion remained unclear. Similar results were obtained in a study combining molecular phylogeography, niche modelling and paleoecological records developed in eastern Amazonia. According to de Lima et al. (2014), extant *M. flexuosa* showed low genetic diversity but significant genetic differentiation among populations from different river basins. This was interpreted in terms of range retraction into refugia during the LGM, and was attributed to increased aridity, as in the classical Neotropical version of the refuge hypothesis. The authors attributed the LGM aridity to the latitudinal shifts of the Intertropical Convergence Zone (ITCZ), but no paleoclimatic data were provided on the magnitude of the aridity shift.

Independent paleoclimatic data indicate that tropical South America was significantly colder and drier than today during the LGM. Indeed, previous studies using noble gases dissolved in groundwater pointed toward a general ~5°C cooling, with respect to present-day temperatures (Stute et al., 1995). Paleorecipitation patterns, as estimated from oxygen isotope records in speleothems, were more heterogeneous due to the existence of an east-west dipole consisting of fairly stable and wetter climates in western Amazonia and more unstable and drier climates in the eastern side (Cheng et al., 2013). The estimated precipitation was generally reduced by almost 60%, as compared to today, but this was not enough for the forests to be turned into savannas dominated by C4 grasses, as deduced from carbon isotope analysis (Wang et al. 2013). How could the reduction in precipitation have affected *M. flexuosa*?

First of all, it is important to stress that *M. flexuosa* grows in a variety of biomes and ecosystems including open savannas with drier and more seasonal climates than those required for lowland rainforest development. Therefore, if the aridity shift did not exceed the forest threshold, as suggested by Wang et al. (2013), it is to be expected that *Mauritia* would be affected less. But even in the case of a hypothetical forest fragmentation within a savanna landscape, as proposed by the RH, this should not have been a problem for *M. flexuosa*, as this species grows well in savanna environments (Fig. 2), as well as in vegetation mosaics with forests, savannas and forest-savanna mosaics (e.g., Urrego et al., 2011, 2016; Rosa et al., 2013; Rull & Montoya, 2014; Mendes et al., 2017; Sander et al., 2022; de Ávila et al., 2023; Hergoualc'h et al., 2024). Moreover, *Mauritia* stands usually replace lowland forests when these experience reductions due to dryness or fire (Urrego, 1997; Montoya & Rull, 2011). Therefore, forest reduction and savanna expansion may even favor *Mauritia* expansion, rather than shrinking its range.

In contrast, LGM cooling could have been more influential. Considering a temperature lapse rate of -0.55-0.60 °C/100 m elevation, which is usual in Amazonia and the surrounding mountain slopes (Zink & Huber, 2011; Rapp & Silman, 2012; Kirkels et al., 2020), a temperature dropping of ~5°C could have represented a lowering of 800-900 m in the upper limit of *Mauritia*. This could have significantly reduced the habitat suitable for this taxon to a short elevation range between the sea level and 100-200 m, likely causing severe range reduction in *Mauritia*, and possibly fragmentation into refugia, as observed in pollen records (Fig. 4). Therefore, the more important environmental constraint for this taxon during the LGM would have not been moisture availability but temperature constraints.

In summary, the case of *M. flexuousa* reduction during the LGM, as shown in paleoecological records, does not fit with the classical view of extended Neotropical aridity with wet refugia, but seems more a matter of a general cooling with warm refugia/microrefugia. This RH framework is not incompatible, but complementary, with the DVH of downward migration of montane species to Neotropical lowlands, with the corresponding changes in forest taxonomic composition. The rapid Holocene expansion coinciding with the EHW and the stabilization during the HTM, along with the western expansion despite the Late Holocene regional drying (Haug et al., 2001), would support the thermal refuge hypothesis for *Mauritia*. This explanation would also be compatible with the evolutionary history of the subtribe Mauritiinae, to which *Mauritia* belongs, which was primarily affected by cooling events (Bogotá-Ángel et al., 2021).

3. The Caribbean Mangroves

Mangroves are forested ecosystems from tropical and subtropical intertidal zones, playing a crucial role in preserving coastal biodiversity and offering essential ecological services. They are also the most significant blue-carbon ecosystems contributing to global warming mitigation. Mangroves grow around the average sea level, developing zonal vegetation gradients from low to high tides, and from saline to oligohaline or freshwaters. They thrive particularly in flat sedimentary terrains and are absent in steep coastal slopes, rocky shores or littoral cliffs. Typical average mangrove elevations range between -1 m to 3.5 m extending from a few hundred m to several km inland, with average slopes between 0.01% and 0.45% (Ellison et al., 2024). Mangrove ecosystems are structured around a reduced number of dominant tree species – the so called mangrove-forming trees – with special morphological and physiological adaptations to saline environments (Tomlinson, 2016).

In the Caribbean region, mangroves cover a total area of approximately 14,700 km², accounting for ~10% of the world's mangrove surface (Bunting et al., 2022) (Fig. 5). The main mangrove-forming trees in the region include the red mangrove (*Rhizophora*, Rhizophoraceae), black mangrove (*Avicennia*, Acanthaceae), and white mangrove (*Laguncularia*, Combretaceae). Additional components, such as the tea mangrove (*Pelliciera*, Tetrameristaceae) and the mangrove fern (*Acrostichum*, Pteridaceae), are also typical but occupy marginal environments. Caribbean mangroves first emerged during the Middle Eocene, initially dominated by *Pelliciera*. However, during the EOT, *Rhizophora* became the dominant mangrove-forming tree. The Neogene period saw increased diversification, ultimately shaping the present-day mangrove composition. During the Quaternary, Pleistocene glacial/interglacial cycles and human activities further shaped the Caribbean mangrove ecosystems. A detailed account of their evolutionary history is available in Rull (2024a).

Quaternary records of Caribbean mangroves correspond mostly to the Holocene, with only a few Late Pleistocene records dated to ~130 ka and ~70-30 ka (Mitchell et al., 2001; González et al., 2008; González & Dupont, 2009). The LGM remains unnoticed, and the earliest postglacial records are from ~12 ka (Pocknall & Jarzen, 2024). Considering the LGM global relative sea level (RSL) drop of 130-134 m below the present (Lambeck et al., 2014; Spratt & Liesecki, 2016), the entire Caribbean continental shelf would have been exposed, thus severely reducing the flat areas (FAs) suitable for mangrove growth. It has been proposed that, in these conditions, the Caribbean mangroves could have survived in restricted flat refugia/microrefugia beyond the shelf break (Fig. 6). However, the lack of paleoecological records of that age hindered testing such hypothesis.

A first approach to the problem consisted of a microtopographical bathymetric image analysis using the Global Multi-Resolution Topography (GMRT) tool (Ryan et al., 2009). The main aim was to locate the most suitable prospects for FAs around -132 m (the average LGM-RSL drop) potentially favoring mangrove growth during the LGM. Using the worldwide elevation averages quoted above (Ellison et al., 2024), the depth range analyzed was -128 to -133 m, and the range of prospective slopes were 0.01% to 0.45%. Using these parameters, a careful examination of the shelf break topography across the entire Caribbean coasts revealed the zones with higher probability of containing FAs suitable for mangrove growth. The further high-resolution analysis of topographical profiles within these areas provided the most suitable prospects for mangrove development (Rull, 2025).

The results of this analysis indicated that, during the LGM, much of the Caribbean coastline was not suitable for mangrove growth, leaving only a few FAs where these ecosystems could have persisted. The most substantial concentration of mangroves was likely located on the northern Trinidad (NT) shelf, which may be seen as the main mangrove refugium during the LGM, and the Cariaco basin (CB) (Fig. 6). Additional suitable locations were small km-scale dispersed areas that could have served as microrefugia for mangroves (Fig. 6). The high-resolution analysis of the larger and best-suited NT potential refugium is presented as an example (Fig. 7). In this area, the most prospective FAs lie in the central sector and decrease toward the east and west, where coasts become steeper. This is illustrated by a central land-sea elevation profile (NTC), where the potential mangrove boundaries span nearly 6 km inland with an average slope of 0.09%. An example of an unfavorable topographical gradient is found on the western side (NTW), where the horizontal space for mangrove growth is less than 200 m, with an average slope of 3.05%. A range of intermediate situations exists across the NT site, including slopes close to the maximum, as shown in an eastern profile (NTE) with an average slope of 0.41%.

The location of the main potential refugial areas (NT and CB) is suggests that, as sea levels rose after the LGM, mangroves likely expanded across the Caribbean coastline, with their primary sources of recolonization being refugia and microrefugia situated in the southeastern region. It is known that surface coastal currents are the main agents for dispersing mangrove propagules (van der Stocken et al., 2019). In the Caribbean, the main surface currents enter through the eastern coasts via the Northern Equatorial Current (NEC) and the Guyana Current (GC) – flowing through the Lesser Antilles and northern Trinidad, respectively – before entering the Gulf of Mexico by the Yucatan Channel (Fig. 5). As this circulation pattern has remained constant since the LGM (Rull, 2025), surface circulation would have been favorable for westward mangrove expansion from the primary NT and CB refugial areas across the Caribbean, with minor contributions from other microrefugia. These preliminary results should be validated with further coring campaigns in the potential refugia/microrefugia identified, to confirm the actual occurrence of mangroves during the LGM.

Again, this is an unconventional approach to the refuge hypothesis in the Neotropics, with the sea-level drop, rather than the climate, as the primary environmental driver. Climatic shifts could also have played a role, but with the available evidence it is not possible to evaluate to what extent. A remaining enigma is the vegetation that occupied the exposed shelf during the LGM. Considering the abovequoted cooling, it would be reasonable to assume that the most temperature-sensitive lowland species – and possibly also those with high thermal tolerance – would have been able to migrate downward and occupy the newly created shelf space for terrestrial biota. One of these species could have been *Mauritia flexuosa*. Once more, the RH and the DVH appear as complementary, rather than opposite explanations. However, paleoecological records to confirm this point remain unavailable. Much paleoecological work is still needed to be done in the Caribbean continental shelf. Such an initiative could benefit from the existing paleoecological and paleoclimatic studies in similar tropical mangrove-bearing environments with emerged continental shelves during the LGM, notably the Indo-Malayan Sundaland shelf (review in Huang et al., 2024).

4. The Pantepui Oscillator

The Pantepui biogeographical province, situated at the top of the Guiana Highlands (GH) (Fig. 1), is one of the few pristine areas remaining in the world, due to their remoteness and inaccessibility. Topographically, Pantepui is the assemblage of the more or less flat summits of ~70 table mountains – the tepuis – ranging from <1 to 1000 km^2, totalizing >5000 km^2, situated between 1200/1500 and 3000 m elevation (Fig. 8). It has been defined as an archipelago of "sky islands" and frequently referred as a "lost world", after the fantastic novel by Arthur Connan Doyle, which was inspired by the GH landscape and remoteness. The pristinity of Pantepui makes this province a unique natural laboratory to study the origin and evolution of Neotropical biodiversity under natural conditions, without direct human influence (Rull, 2010). The uniqueness, biodiversity and endemism of Pantepui organisms and the communities they form are outstanding. Plants are, by large, the most diverse organisms (~2600 species) and amphibians are those with more endemic species (55%), the other groups usually ranging from 30 to 40%. The Pantepui ecosystems are unparalleled in other Neotropical regions. See Rull et al. (2019)

and Rull & Vegas-Vilarrúbia (2020) for an updated account of Pantepui life and environmental features.

As usual, the current Pantepui biota is the result of a long ecological and evolutionary history, although in this case most inferences come from present biogeographical patterns. This is due to the absence of sediments between the Precambrian and the Quaternary and the scarcity of molecular phylogenetic and phylogeographic studies available, due to the difficulty of obtaining fielwork permits (Rull & Vegas-Vilarrúbia, 2008). In summary, the different hypothesis advocated to explain the origin and evolution of the Pantepui biota may be reduced to the classical biogeographical debate between vicariance vs. dispersal (review by Rull, 2019). Regarding the Quaternary, the RH has also reached the GH. Based on biodiversity and endemism patterns of vascular plants, Steyermark (1979) proposed that Pantepui, as a whole, could have been a wet refugium during th LGM. However, the lack of pre-Holocene peats suggested that LGM climates atop the tepuis were arid, which was incompatible with the purported Pantepui wet refugium (Schubert & Fritz, 1995; Schubert et al., 1994).

Further paleoecological studies demonstrated that a number of temperature-sensitive tepuian species migrated upward and downward following warmer and cooler climates, respectively, during the Holocene (Rull, 2004a, b; Rull & Montoya, 2017). This confirmed previous insights based on the current range of medium-elevation Pantepui species (Steyermark & Dunsterville, 1980), and suggested that the vertical displacement during the LGM would have been greater. Further studies developed immediately south of Pantepui recorded the presence of tepuian elements from montane forests – e.g., *Podocarpus*, *Hedyosmum*, *Wenmannia*, *Alnus* – in the surrounding lowlands during the LGM. This was consistent with a 1000-1100 m downward displacement of these sensitive species and a 5-6°C temperature drop, as recorded by independent methods for Amazonian lowlands (Bush et al., 2004). Therefore, an approximate average downward migration potential of 1100 m, characteristic of the Neotropics (Farrera et al., 1999), was adopted for tepuian thermal-sensitive species.

Once in the lowlands, these species not only changed lowland forest composition but were able to disperse horizontally and eventually climbing to other tepuis during postglacial times (Fig. 9). Other species, situated more than 1100 higher than the surrounding lowlands/uplands, would have been "trapped" in the tepui summits without the possibility of reaching the lowlands. It has been estimated that >70% of the vascular flora would have been able to move among the tepuian summits (Rull & Nogué, 2007). In this way, both vicariance and gene flow would have had their role in the diversification of Pantepui biota during the Pleistocene (Rull, 2005).

This view is more consistent with the DVH and suggests that the Pantepui biota, as well as that of the surrounding lowlands/uplands, could have significantly varied across the Quaternary. It should be added that total annual rainfall in Pantepui varies from 2500 to >3500 mm (Zink & Huber, 2011) and even a very unlikely decrease of 60%, as estimated for Neotropical lowlands during the LGM (Wang et al., 2013), would be insufficient to promote aridity, as formerly proposed by Schubert et al. (1994). The enigma here is the biota that occupied the tepui summits during glacial phases, as no elevations above 3000 m are available from where species could have migrated downward. It has been suggested that glacial summits could have supported species with high temperature tolerance, other unknown species now extinct – the so called "glacial ghosts" (Rull, 2007) – and possibly Andean species that would have been able to cross the Orinoco basin during glacial coolings (Rull et al., 2019). Similar LGM teleconnections have been proposed for several Andean forest genera known to occur in the Brazilian Atlantic Forest (Pinaya et al., 2024) (Fig. 1). To address this novel dynamic perspective of Pantepui, a model called the Pantepui oscillator (PO) was proposed. This model should be viewed as a hypothesis to be tested in the future with paleoecological studies, if finally, Pleistocene sediments do exist and are found atop the tepuis.

The PO dynamic model is based on a fixed element, topography, and two shifting components: climate and biota (Rull & Vegas-Vilarrúbia, 2019). In the current Pantepui, these three elements coincide, as this biogeographical province was defined using current topography, climates and biota. However, during a glaciation, these three components disassemble, as the topographic Pantepui remains but the other two migrate downward (Fig. 10). Such migration, however, is different for the climatic and the biotic Pantepui. Indeed, whereas the climatic Pantepui migrates in a more or less homogeneous fashion following the temperature lapse rate, the species of the biotic Pantepui migrate at different rates, according to their specific thermal requirements, and following the available topographic corridors. The same is true for the upward interglacial migration. This creates a complex and dynamics spatiotemporal scenario that, repeated for ~40 times across ~70 tepuis and their surrounding lands, has modelled the present-day Pantepui biota. A corollary is that the current Pantepui could be one of the ~40 pantepuis that have existed during the Quaternary, due to the idiosyncratic responses of the different species to glacial-interglacial shifts of changing intensity and duration.

5. Disequilibrium Dynamics

It is not unusual the perception of the current interglacial situation in which we live, as the "normal" state of biomes and ecosystems, and the glacial conditions as transient bottlenecks that species have to endure to avoid extinction. In this way, the *Mauritia* warm refugia, the mangrove topographical refugia and the disassembled Pantepui may be viewed as unstable conditions to be equilibrated in the next interglacial. However, the Quaternary is actually a glacial period during which the Earth has been glaciated 80% of the time (Willis & Whittaker, 2000). Therefore, glaciations, rather than interglacials, can be considered the norm (Bush et al., 2001). In addition, there is a thermodynamic argument that changes our perception of glacial vs. interglacial equilibrium dynamics.

Although glacial-interglacial cycles are governed by symmetrical astronomically-driven solar cycles of energy input to the Earth – i.e., the Milankovitch cycles (Berger, 1988) – paleotemperature records from ice cores show a typical asymmetric pattern for glacials and interglacials. Indeed, whereas interglacial warmings are short and abrupt events, glacial coolings are gradual and extended trends (Fig. 11). Interglacial warmings occur at the end of glaciations – this is why they are also known as terminations – at faster rates than insolation increases. This is due to the action of magnification drivers, such as changes in albedo and atmospheric CO_2 concentration, that exacerbate the response of climatic system to solar forcing (Ellis & Palmer, 2016). Therefore, interglacials are triggered by the abrupt inputs of extra energy to the climatic system, and when these inputs cease, the system gradually returns to its glacial state. In simple thermodynamic terms (Hill, 1960), interglacials are short unstable states driven by external energy inputs and glacials represent the relaxation of the system to maximum entropy levels, once the external energy input ceases. Thus, the Quaternary may be viewed as a period characterized by a long-term stable glacial climate interrupted by short and abrupt unstable interglacial warmings (Bush et al., 2001). Coming back to the examples discussed above, warm refugia for *Mauritia*, topographic refugia for mangroves and Pantepui disassembly could be considered the stable states, whereas *Mauritia* and mangrove expansion, along with Pantepui coupling, would be transient and unstable states to be stabilized, or not, in the next glaciation.

This situation fits within the concept of nonequilibrium dynamics introduced by Hutchinson (1957), who argued that competitive exclusion leading to extinction of most species and the dominance of one or few of them require a stable environment. In contrast, small environmental changes, although short-lived, could change competitive relationships, thus contributing to spatiotemporal niche segregation and favoring diversification. Davis (1981) used paleoecological evidence to support this idea in postglacial expansion of North American forests. According to this author, the occurrence of constant environmental variations at diverse spatial and temporal scales lead to dynamic disequilibrium (or nonequilibrium dynamics) in which plant communities are permanently modified without ever reaching equilibrium. The Quaternary shifts of *Mauritia*, the Caribbean mangroves and Pantepui, among many others, could be a good example of this idea. However, contrary to the common perception, interglacials would be the external disturbances, whereas glacials would be the stabilizing phases.

6. Global Warming and Sea-Level Rise

In the examples discussed here, temperature and eustatic shifts have been identified as the main drivers of biogeographical and ecological change. Therefore, it could be asked what could be the situation of *Mauritia*, the Caribbean mangroves and Pantepui in a future warmer world with rising sea levels. Many models coincide in that the interglacial in which we live, the Holocene, will be longer than usual due to the anthropogenic global warming.

Some of these models predict that the next glaciation could be delayed by 40,000 years (Herrero et al., 2014). Other prognosticate that the increase in atmospheric CO_2 concentration will surpass the effect of astronomical solar cycles, which are the pacemakers of the glacial-interglacial cyclicity, thus indefinitely interrupting this cyclicity for at least a million years (Haqq-Misra, 2014). A third group of more extreme predictions mentions a point-of-no-return threshold beyond which glacial-interglacial cycles would be interrupted indefinitely to enter in a permanent "hothouse" Earth characterized by high temperatures with little latitudinal differences, with the poles devoid of ice, and sea levels significantly higher than at present. Steffen et al. (2018) proposed that an increase of only 2°C above preindustrial times would be enough to provoke a cascade effects of positive feedbacks eventually resulting in a hothouse Earth. At least 15 hothouse phases elapsing up to several million years have been documented in the Earth's history (Kidder & Worsley, 2014). The ltest of these hothouse states occurred in the Early Eocene, when temperatures were ~16°C higher than at present and relative sea levels ~60 m above current ones (Miller et al., 2020; Westerhold et al., 2020).

For *Mauritia*, rising temperatures and the smoothing of the thermal latitudinal gradient would imply the possibility of colonizing higher elevations, likely in the Andes and the Guiana Highlands, and expanding its latitudinal range. However, the extent to which this would be possible depends on the niche features of other species and the ecological relationships of *Mauritia* with them. In any case, *Mauritia* could be favored by the global warming, provided hydroclimatic conditions are suitable for maintaining its preferred freshwater-flooded habitats. Fossil data indicates that the Mauritiinae have been tropical since their Cretaceous origin, and there is no evidence for latitudinal expansion, not even during hothouse Earth states (Bogotá-Ángel et al., 2021). Therefore, past analogues for a purported future expansion are lacking.

Mangroves could also be favored in a warmer Earth with higher sea levels, but in this case the land topography and the predicted increase in meteorological hazards – especially tropical cyclones or hurricanes, which are the most destructive phenomena for mangroves (Burgess, 2018), would be constraining factors, at least locally. Contrary to *Mauritia* and its phylogenetic relatives, fossil pollen evidence supports worldwide mangrove expansion during the Early Eocene under hothouse conditions. In those times, the northern boundary of mangroves (now at ~30°N) was situated 80°N, close to the north pole, which was deglaciated (Popescu et al., 2021).

In the case of Pantepui, the situation is different, because interglacials are times of enhanced extinction by habitat loss in mountaintops (Rull, 2005). Indeed, cold adapted species are unable to migrate upward during warmings due to the lack of terrains above 3000 m. The flat topography of the tepui summits favors biodiversity accumulation and the development of larger populations than in more conical mountains. Therefore, biodiversity depletion by habitat loss would be comparatively much greater atop the tepuis. It has been estimated that 75-83% of Pantepui vascular flora could become extinct by habitat loss at the end of this century, under the IPCC temperature predictions for the area (Nogué et al., 2009). Of them, 28-54% correspond to endemic species, which means their worldwide extinction. It was also estimated that a temperature increase of 9°C – not unusual in hothouse conditions – would be enough for the total Pantepui flora to become extinct (Rull & Vegas-Vilarrúbia, 2006). This would not only lead to the total extinction of the Pantepui vascular plants but also of all other species depending on them for its development.

7. Synthesis and Further Work

The three examples discussed here account for LGM vegetation trends and patterns across two spatial (elevation and longitude) and two temporal (climate and sea-level shifts) environmental gradients. The elevation gradient ranges from the depth of the Caribbean continental shelf (-132 m) to the top of the Guiana Highlands (~3000 m), whereas the longitudinal gradient includes from western to eastern Amazonia. The temporal gradients go from the LGM cooling in tropical South America and the Caribbean lowstand, to the Holocene warming and sea-level rising trends. The vegetation dynamics across these gradients also defined biogeographic and ecological spatiotemporal gradients modulated by the idiosyncratic responses of species to environmental change. Altogether, this defines a complex scenario of environmental forcing and biotic reaction in a framework of disequilibrium dynamics that has shaped modern ecosystems.

Low LGM temperatures and sea levels determined downward biotic displacements including mountain species reaching the lowlands, lowland species like *Mauritia* being refugiated near the sea level, and possibly in the exposed continental shelf, and mangroves being reduced to a few refugia/macrorefugia situated mainly in the southeastern Caribbean shelf break. The ecosystems that occupied the highest GH elevations and the Caribbean continental shelf during the LGM remain unknown, and a number of them have probably become extinct (glacial ghosts). Overall, biogeographical ranges of sensitive species were depressed, which changed the composition of lowland forests and increased discontinuities in some taxa and ecosystems, especially in *Mauritia* and mangroves.

Postglacial warming and sea-level rise favored the expansion of *Mauritia* and mangroves, along with the upward displacement of sensitive species to the mountains, which changed the composition of lowland and slope forests. Dispersal across the lowlands during the LGM would have favored taxonomic interchange and gene flow among tepuis, and warming could have led to extinction of sensitive high-elevation LGM species by habitat loss. This would have significantly change the composition of the Pantepui biogeographical province, as currently defined. Also, the glacial-interglacial variability and the associated diversification increase could have led Pantepui to act as a "biodiversity pump" for the surrounding lowlands (Rull, 2005).

The recurrence of the glacial-interglacial cycles across the Pleistocene has shaped modern biomes and ecosystems. However, these repetitions have not been identical, as they have occurred not only variations in extent and intensity (Raymo, 1994), but also biotic reorganizations and disequilibrium dynamics in the environmental-biotic relationships. As mentioned, ecological reorganizations were the result of species' idiosyncrasy in the response to environmental shifts, together with lowland migration across extensive areas – i.e., the Orinoco and Amazon basins – during the long glacial phases. Disequilibrium dynamics was the result of glacial relaxation and entropy increase, aimed at reaching a stable state, after short-lived and unstable interglacial external energy inputs. Whether or not the equilibrium is attained depends on the particular features of each glacial-interglacial cycle and the species involved.

While the exact magnitude remains unknown, most models predict that the next glaciation may be delayed for long time, from tens of millennia to millions of years. Some predict that glacial-interglacial cycles could be interrupted indefinitely. The maintenance of a more or less permanent interglacial stress would not be due to changes in solar energy, as it is expected that the astronomical cyclicity remains the same, but of anthropogenically-driven amplification feedbacks, notably the increase in atmospheric greenhouse gas concentrations. In this situation, mangroves could expand until the polar regions, as it occurred in the latest Early Eocene hothouse state, and the whole Pantepui vascular flora, along with the dependent biota, may become extinct. The destiny of *Mauritia* remains uncertain.

Many of the above ideas and proposals need to be tested with further paleoclimatic and paleoecological studies, ideally on records encompassing the entire Pleistocene. As mentioned above, some exceptionally long records have been retrieved in the Neotropics. In the case of the Caribbean, the Cariaco records have been instrumental to infer the main Pleistocene climatic and oceanographic features of the area (Haug et al, 1998; Yarincik & Murray, 2000). However, paleoecological mangrove records are limited to a short period before the LGM (González et al., 2008; González & Dupont, 2009). In addition to come back to the stored cores to check whether there is still material useful for paleoecological research, coring other potential refugial areas, such as the northern Trinidad shelf, would be highly recommended.

The Bogotá record, which contains a complete Pleistocene sequence, has served to reconstruct the glacial-interglacial oscillations of the north-Andean forests and the highland páramos, thus providing an exceptional reference record for the South American tropics (Hooghiemstra, 1984; Torres et al., 2013). After decades of paleoecological prospecting, finding similar records in other Neotropical mountain ranges and lowlands/uplands has been unsuccessful. However, continued efforts in this direction are worth to be done. More than four decades ago, Schubert (1980), based on seismic profiles, proposed that the sediments of Lake Valencia, at ~400 m elevation (Fig. 1), could contain a record of at least the last 520 ka in the uppermost 300 m. To date, only the first ~7 m, corresponding to the Holocene, have been cored and studied paleoecologically (Bradbury et al., 1981; Binford, 1982; Leyden, 1985).

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Figure captions

Figure 1. Study areas of this paper (yellow boxes) in the Neotropical context. AF, Brazilian Atlantic forests; BB, Bogotá basin; CB, Cariaco basin; GH, Guiana Highlands; LV, Lake Valencia.

Figure 2. Examples of *Mauritia flexuosa* from the Gran Sabana region (Venezuela). A) Light palm stands around a lake. B) Dense monospecific gallery forest surrounded by savanna vegetation. The different colors in savanna vegetation are due to different the stages of vegetation regeneration after frequent fires. Photos: V. Rull.

Figure 3. Present distribution of *Mauritia flexuosa*. Downloaded from the Global Biodiversity Information Facility (GBIF) (https://www.gbif.org/; last accessed Jan 28, 2025).

Figure 4. Map of northern South America showing the localities containing *Mauritia* pollen in their Late Pleistocene and Holocene sedimentary records. The coring sites are indicated in blue – see Rull & Montoya (2014) for details and references – and the *Mauritia* pollen percentages in red.

Figure 5. Map of the Caribbean mangroves (green patches), according to Bunting et al. (2022). Downloaded from NASA Landsat 5-TM (https://earthobservatory.nasa.gov/images/47427/mapping-mangroves-by-satellite). The refugial areas identified by the microtopographical analysis are represente as red dots and the superficial currents as blue arrows. Refugia/microrefugia: CB, Cariaco Basin; NC, northern Colombia; NT, northern Trinidad; WH, western Hispaniola. Currents; CC, Caribbean current; GC, Guyana current; NEC, northern Equatorial current.

Figure 6. GMRT map of the Caribbean seafloor indicating the -132 m isobath, representative of the LGM relative sea level position. Note that this isobath coincides with the shelf break, indicating that the whole continental shelf (light gray) was exposed during the LGM. The most prospective zones used in the microtopographical analysis are shown by yellow boxes. CB, Cariaco Basin; NC, northern Colombia; NT, northern Trinidad; WH, western Hispaniola.

Figure 7. Magnification of the northern Trinidad shelf break (NT) showing the isobaths between -128 and -133 m at meter resolution, and representative examples of LGM coastal profiles (yellow lines) from west to east. The space available for mangrove growth is highlighted by a thick green line in the below profiles. Note that the NTW profile is a steep coast unsuitable for mangrove growth, whereas the NTC and NTE profiles fall within the coastal slope suitable for mangrove development (0.01%.0.45%). Methodological details in Rull (2025). Abbreviations: AS, average slope; LGM-RSL, relative sea level during the Last Glacial Maximum; LML, lower mangrove limit (-133 m); UML, upper mangrove limit (-128 m).

Figure 8. Examples of tepuis and tepuian massifs. A) The Roraima massif viewed from the Venezuelan Gran Sabana (photo: V. Rull). B) The Roraima summit and upper cliffs (photo courtesy of Javier Mesa). C) The Upuigma tepui and the surrounding Gran Sabana uplands (photo: V. Rull). D) the Ilú-Tramén massif (photo: V. Rull). See Rull et al. (2019) for details.

Figure 9. Schematic representation of the diversification model in Pantepui consistent with the disturbance-vicariance model. The tepui summits are in dark red and the vertical migration of sensitive species is represented by brown arrows. Simplified from Rull (2005).

Figure 10. The Pantepui oscillator. The orographic (green, climatic (pink) and biotic (yellow) Pantepui components assemble during interglacials (like the current Holocene) and disassemble during glacials by differential downslope migration. Redrawn from Rull & Vegas-Vilarrúbia (2019).

Figure 11. Temperature anomalies (blue line) with respect to the present average (dotted line) during the last four glacial cycles as recorded in the Vostok ice core (Antarctica). Interglacials are highlighted by gray bands. Note that the onset of interglacial warmings are abrupt, whereas glaciations exhibit a gradual temperature decrease (red lines) spiked by minor interstadial events (IS). Modified from Petit et al. (1999).

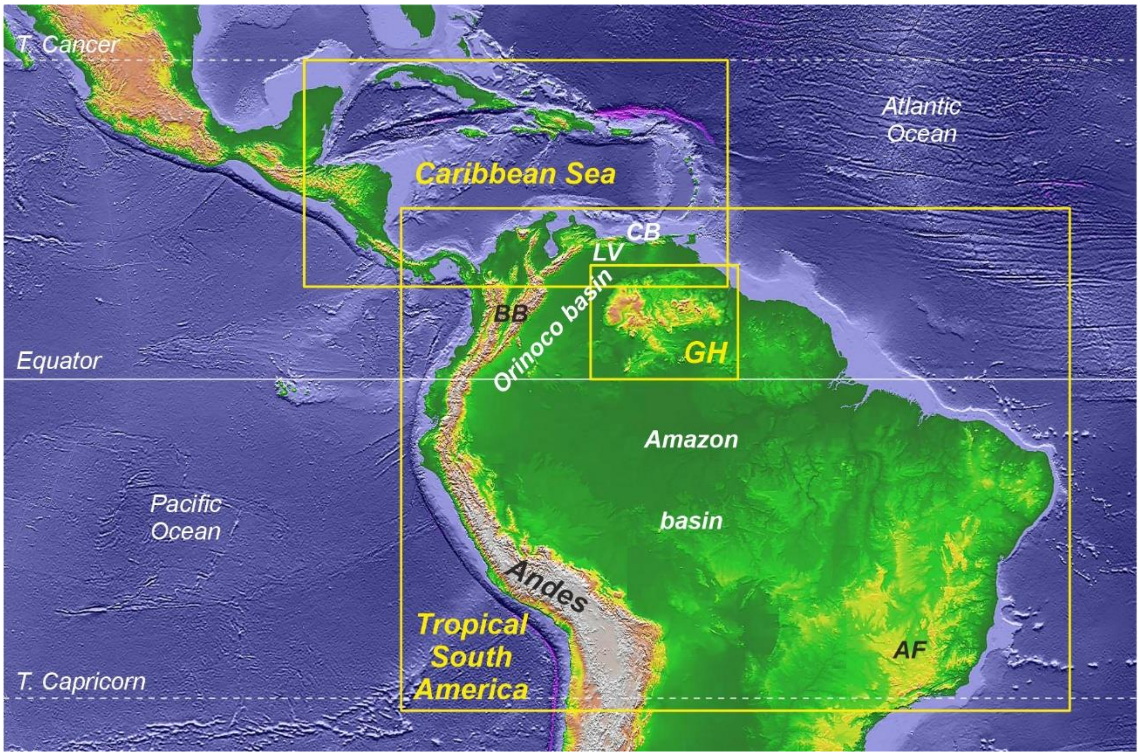

Figure 1

Figure 2

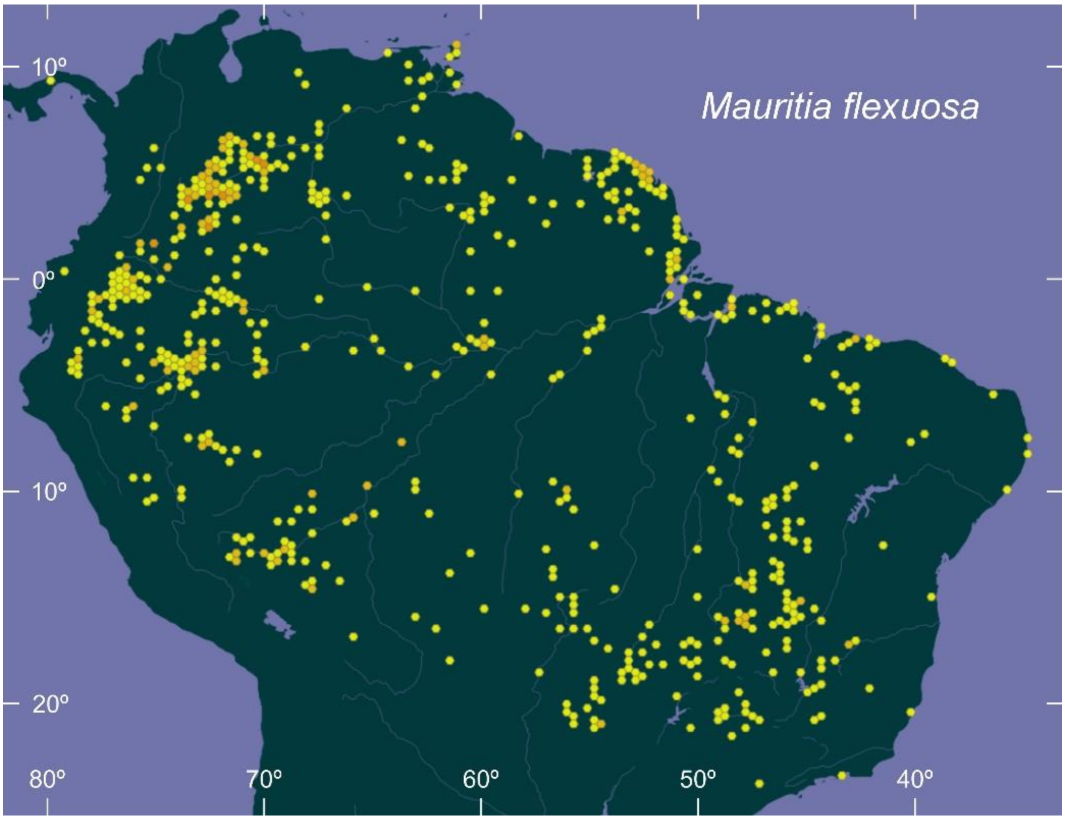

Figure 3

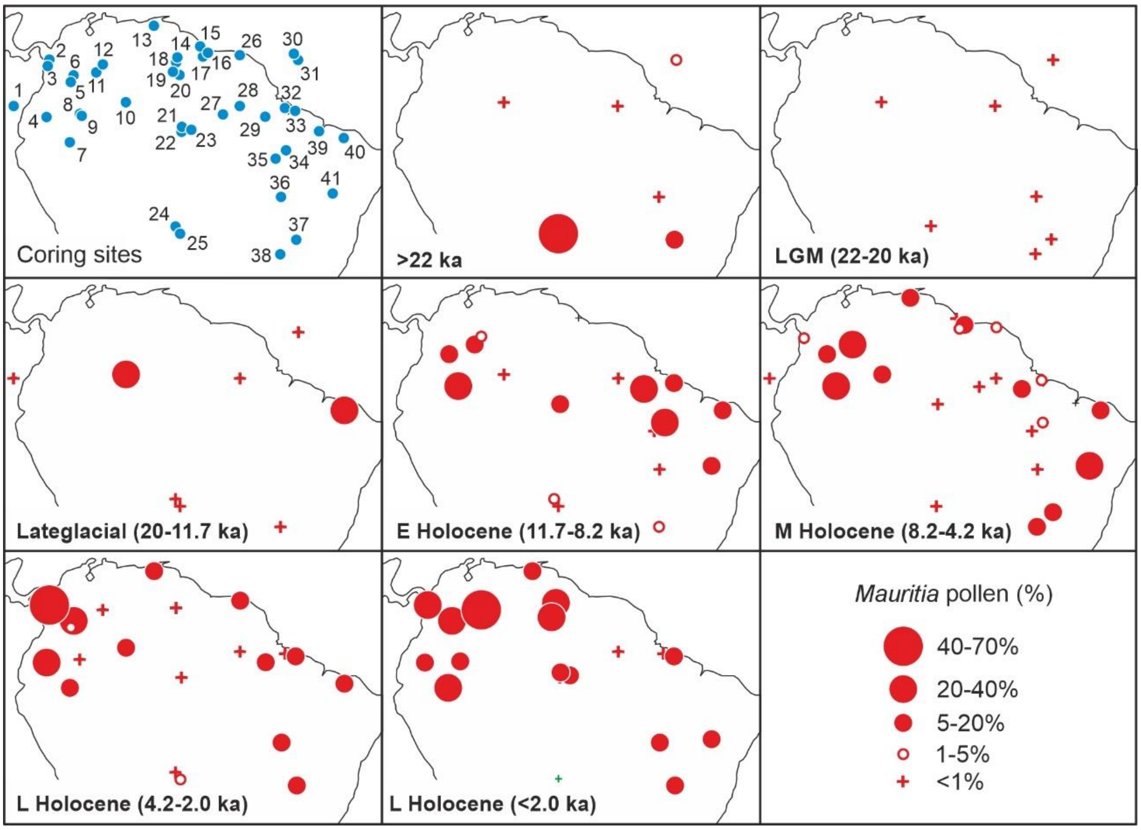

Figure 4

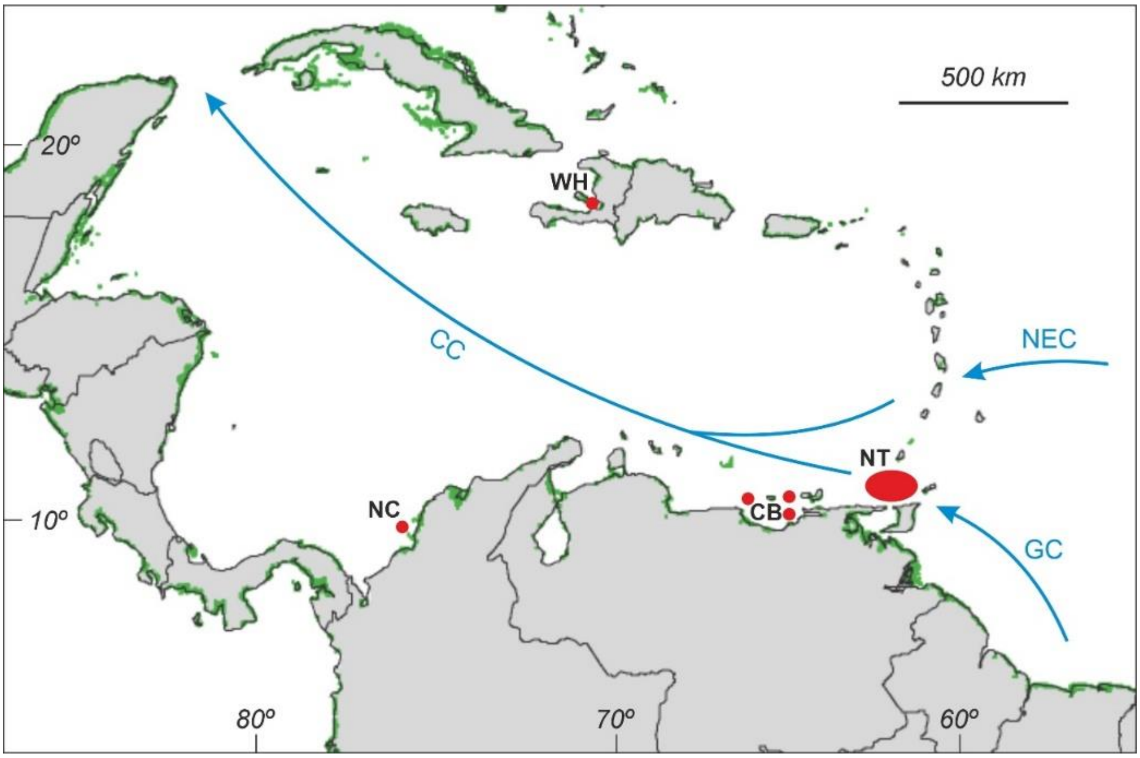

Figure 5

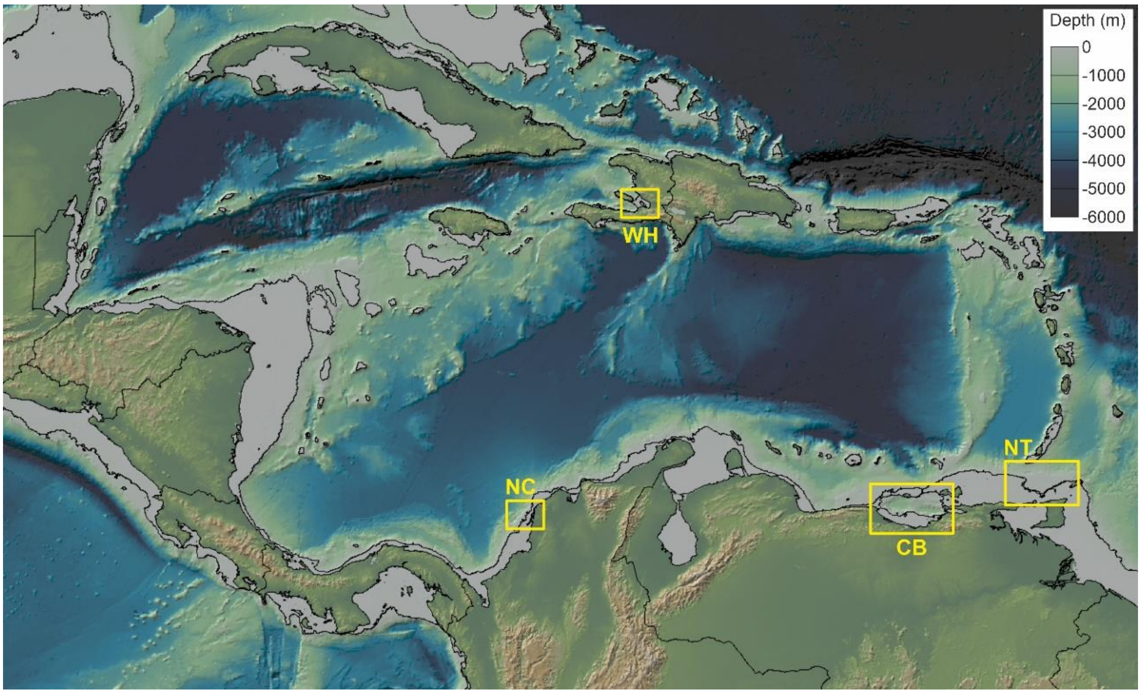

Figure 6

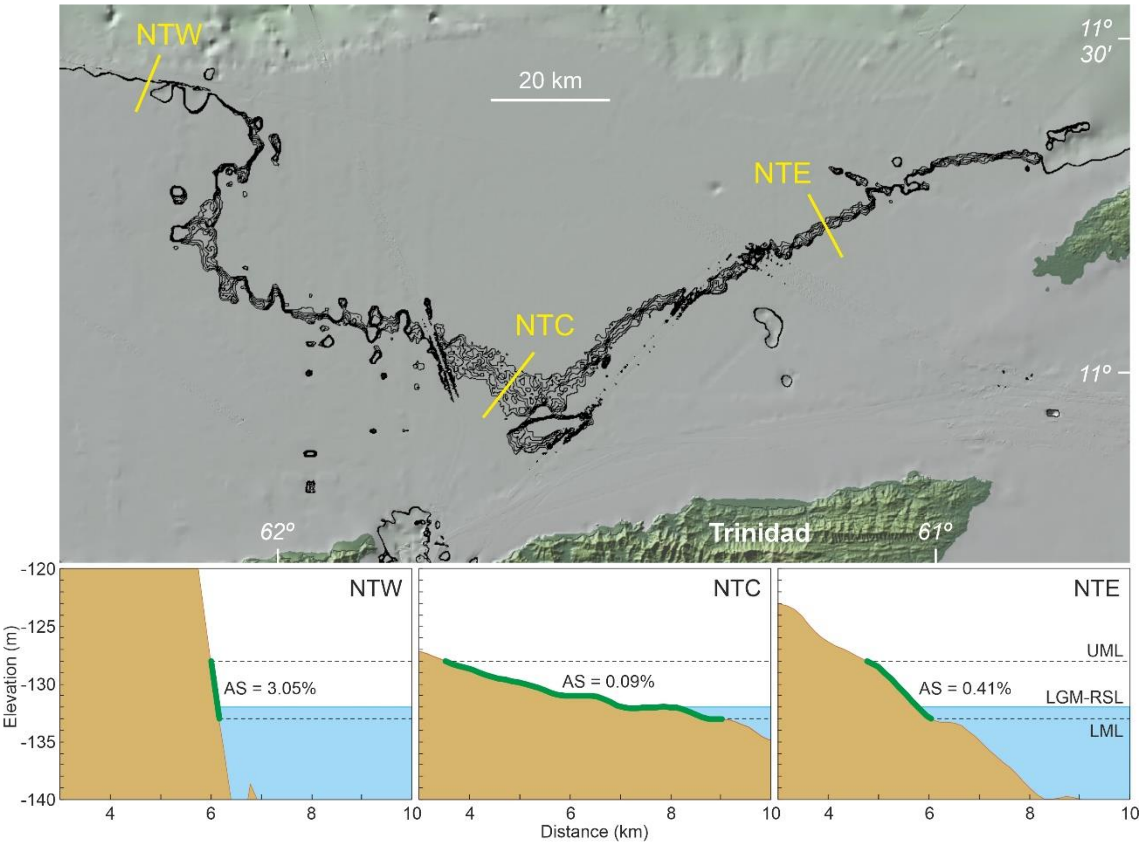

Figure 7

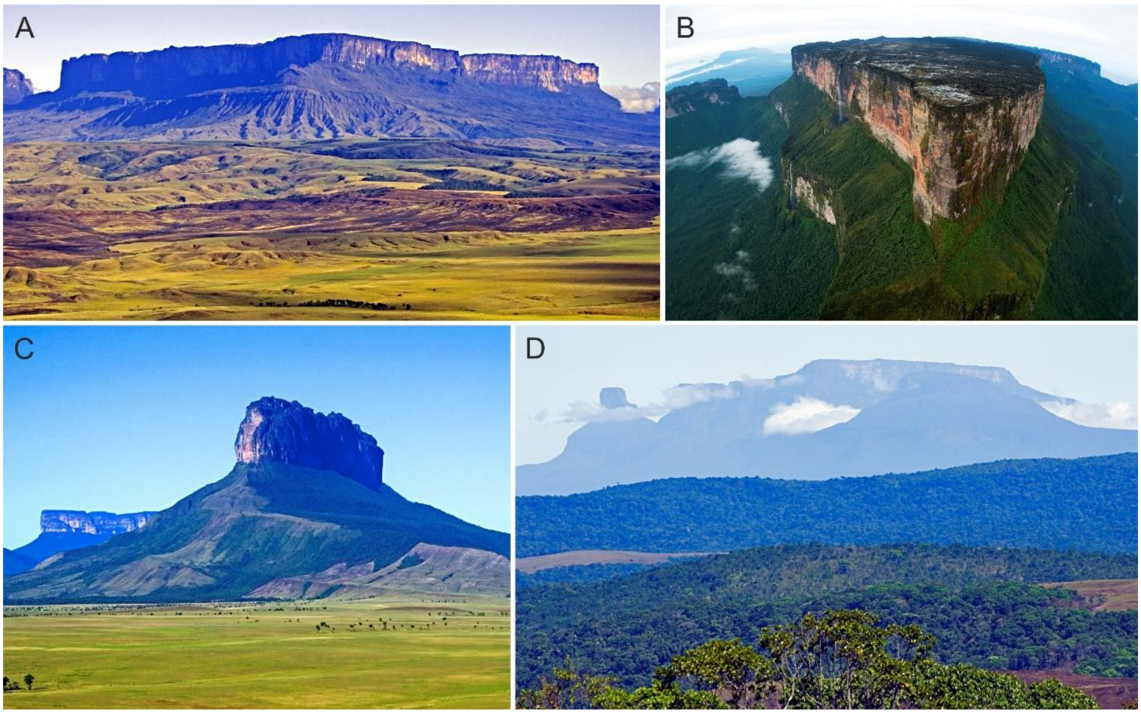

Figure 8

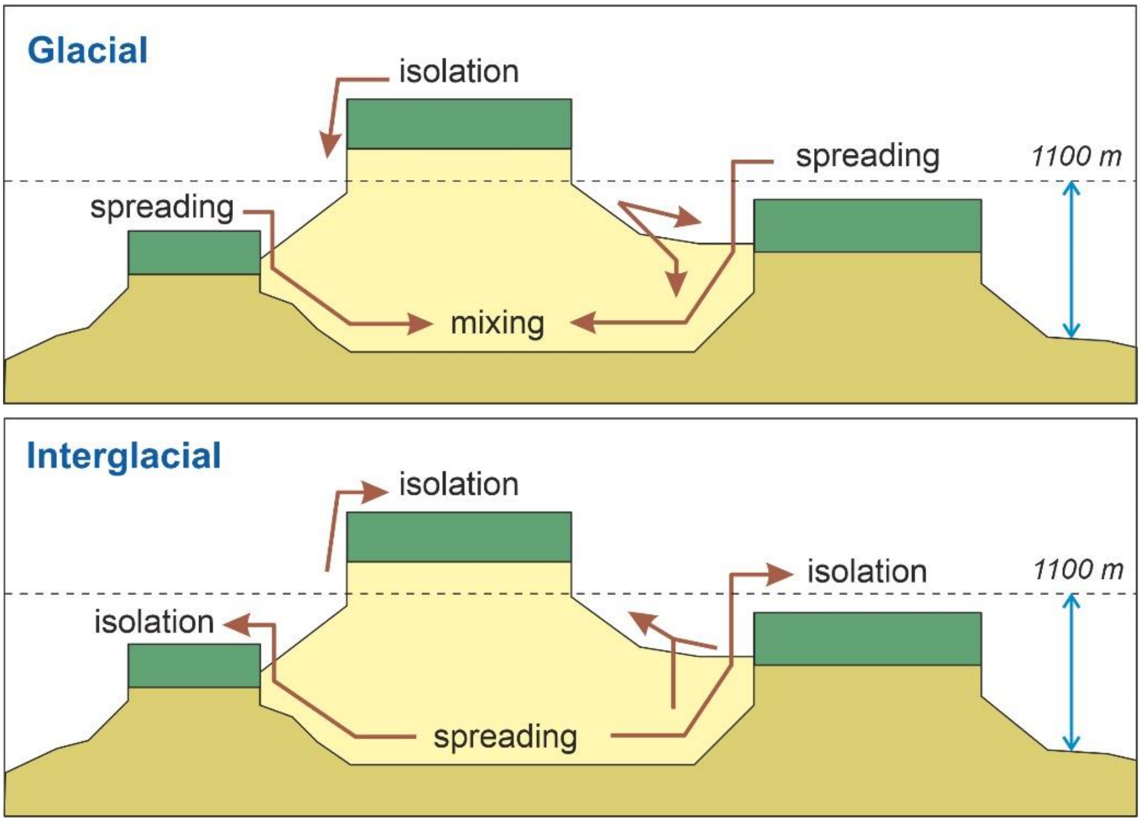

Figure 9

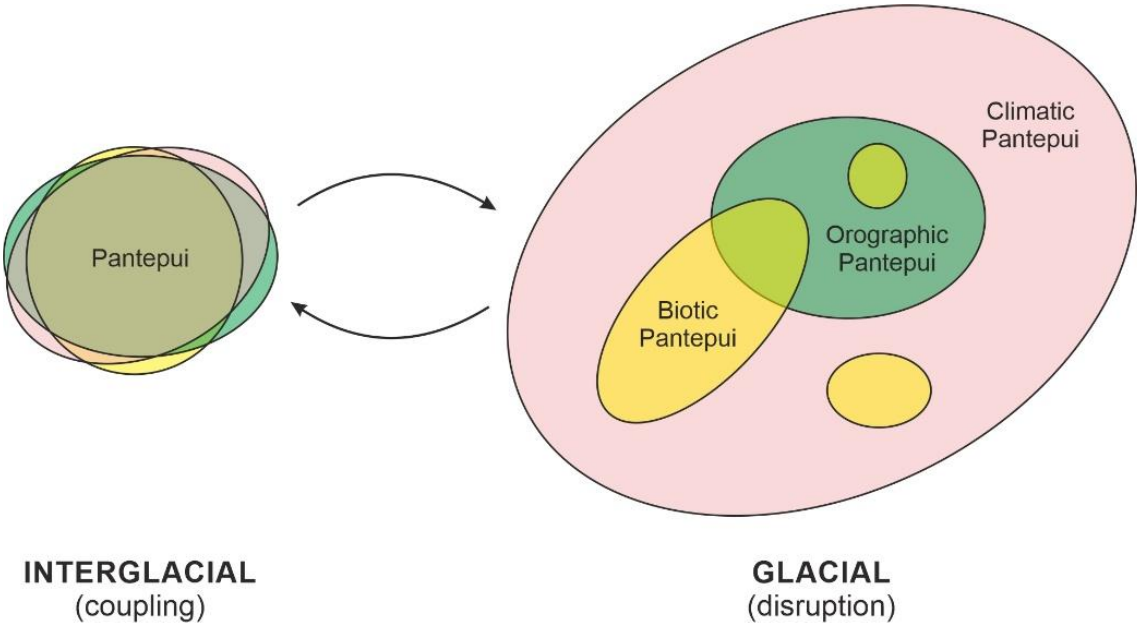

Figure 10

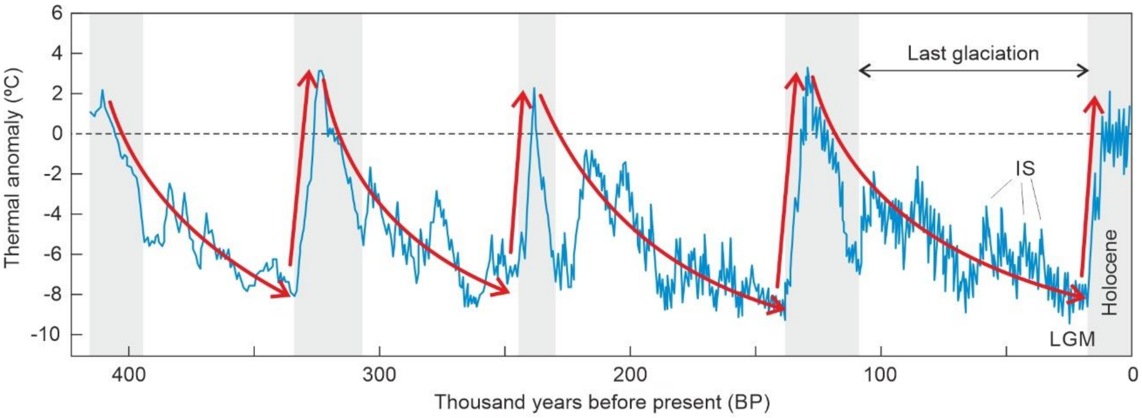
6
4
2
0
-2
-4
-6
-8
-10
Thermal anomaly (ºC)
400
300
200
100
0
Thousand years before present (BP)
Last glaciation
IS
LGM
Holocene

Figure 11